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Comparative Morphology of *Atalodera* spp. and *Thecavermiculatus* spp. (Heteroderidae) with Scanning Electron Microscopy[1]

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Abstract: SEM examination of second-stage juveniles (J2) and adults of *Atalodera ucri, A. lonicerae* (syn. *Sherodera lonicerae*), *Thecavermiculatus* sp. (undescribed new species), *T. andinus,* and *T. crassicrustatus* revealed new characters. A primitive en face pattern with six separate lips occurs in J2 of *Thecavermiculatus* spp. examined and in about half the polymorphic *A. lonicerae.* A derived en face pattern with fused adjacent submedial lips occurs in the other half of *A. lonicerae* and all *A. ucri.* Posteriorly, the J2 head of all species is annulated. The primitive en face pattern also occurs in males of *A. lonicerae* and *Thecavermiculatus* spp., and posteriorly the head of these species consists of plates. Fewer plates occur rarely in males of *A. ucri.* Males of *A. ucri* have a derived en face pattern where lips are fused and the head is annulated. Fusion of lips occurs rarely in males of *A. lonicerae.* Females of all species have similar derived en face patterns. En face patterns of J2 and males of *Atalodera* and *Thecavermiculatus* may aid in species identification and to elucidate intergeneric relationships, but en face characters shared by the two genera are primitive and are not useful for demonstrating monophyly. Perineal region of females indicates the closeness of the vulval–anal distance, as a derived character, which is shared by *Atalodera* and most *Thecavermiculatus* spp. suggesting possible monophyly. *T. andinus,* while having a similar en face pattern to J2 of other *Thecavermiculatus* species, lacks the derived character of the perineal region. Phasmid openings were not observed in adults of any of the species examined.

Key words: en face pattern, perineal region, phasmid, phylogeny, SEM, systematics, vulva.

Atalodera Wouts and Sher, 1971 was proposed for *Atalodera ucri,* a heteroderid with females that do not form cysts, have a lace-like cuticle pattern, and have the anus and vulva located on a terminal prominence (16). These characters are shared with *Sherodera* sensu Wouts, 1973 which was diagnosed by females with a distinct rounded dorsal vulval lip and males with longitudinally striated head annules (15). Luc et al. (8), in their reevaluation of Heteroderidae classification, considered the diagnostic characters of *Sherodera* insufficient to justify a separate genus and placed the only species, *Sherodera lonicerae* in *Atalodera. Thecavermiculatus* Robbins, 1978 (13) which shares many characters with *Atalodera* has at least three nominal species (3,7,13) and has been distinguished from *Atalodera* by little or no terminal prominence on females and retention of second-stage juveniles (J2) in females.

Luc et al. (8) considered the classification of Heteroderidae as unstable and artificial because of sparse data, including comparative morphology. To increase the available data, we initiated comparative SEM morphological studies on Heteroderidae (11,12). In this study, en face patterns, lateral fields, body annulations, and sensory openings of J2 and adults of *A. ucri, A. lonicerae, Thecavermiculatus* sp., *T. andinus,*

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TABLE 1. Species and numbers of *Atalodera* and *Thecavermiculatus* examined and their source.

Nematode	Host	Location	Number examined
Atalodera ucri Wouts and Sher, 1971	Golden bush, *Haplopappus palmari* Gary	University of California campus, Riverside	300 juveniles 30 males 80 females
A. lonicerae (Wouts) Luc et al., 1978	Honeysuckle, *Lonicera involucrata* (Richards) Banks ex Spreng	Temecula, California	350 juveniles 80 males 60 females
Thecavermiculatus sp. (undescribed species)	*Festuca dertonensis* (All.) Asch. and Graebn.	Tomales, California	200 juveniles 20 males 60 females
T. andinus Golden et al., 1983	*Oxalis tuberosa* Mol.; *Chenopodium quinoa* Willd.	Lake Titicaca, Puno, Peru	250 juveniles 3 males 80 females
T. crassicrustatus	Dunegrass, *Elymus mollis* Trin.	Aleutian Islands, Alaska	6 juveniles 1 male (SEM) 6 males (LM) 2 females

and *T. crassicrustatus*[4] were compared using SEM. Characters revealed in these studies can be used in identification as well as in defining and testing hypotheses of phylogeny of Heteroderidae with the aim of developing a stable and natural taxonomy.

MATERIALS AND METHODS

Second-stage juveniles, males, and females of *A. ucri, A. lonicerae, Thecavermiculatus* sp., *T. andinus,* and *T. crassicrustatus* were collected from type localities (Table 1). These specimens (except *T. andinus* males) were processed for SEM by either critical point drying (cpd) (11) or glycerin infiltration (gly) (14). Relative advantages of the two methods were previously reported (11). Although males of *T. andinus* were not available for SEM study, three paratypes of slide UCDNC No. 2108 were made available for light microscope examination. Terminology used for en face patterns is based on interpretation of variations as modifications of a basic pattern, in which the labial disc is encircled by six lips (two lateral and four submedial) of the first head annule (11).

RESULTS

Head morphology: En face patterns of J2, males, and females of *Atalodera* and *Thecavermiculatus* species are variable. The J2 en face pattern of *A. ucri, A. lonicerae, Thecavermiculatus* sp., *T. andinus,* and *T. crassicrustatus* has a labial disc which is dorsoventrally ovoid (Figs. 1C, F, G, J, M; 2C). Adjacent submedial lips of *A. ucri* J2 are fused, although there is a dorso-ventral indentation in the area of fusion. Lateral lips are partially fused with submedial lips but are separate from the labial disc (Fig. 1C). Posteriorly, the head has one incomplete and one complete annulation (annulation = the groove between ring-like annules). The incomplete annulation occurs only on the lateral sides (Fig. 1A, B). However, a few individuals exist in which the head region posterior to the lip annule has only two complete annulations.

Adjacent submedial lips of *A. lonicerae* J2 are either fused or separate (Fig. 1F, G). Sometimes an individual has two adjacent submedial lips fused and the other two separate (Fig. 3C). When the adjacent submedial lips are fused, no indentation is observed in the area of fusion (Fig. 1E, G). Lateral lips are partially fused with the labial disc but are separate from submedial lips (Fig. 1D, F, G). Posteriorly, the head has one incomplete and two complete annulations. The incomplete annulation occurs only on the lateral sides (Fig. 1D, E). In J2 of *Thecavermiculatus* sp., *T. andinus,* and *T. crassicrustatus,* adjacent submedial

[4] *Thecavermiculatus* sp. is very similar to *T. gracilancea* which we were unable to recover from the type locality. Although SEM morphology of the two populations is nearly identical (13), minor differences occur and may justify morphometric description of the former as a separate species (R. T. Robbins, pers. comm.). *T. crassicrustata* and *T. gracililancea* were corrected to *T. crassicrustatus* and *T. gracilancea,* respectively, by Fortuner (6).

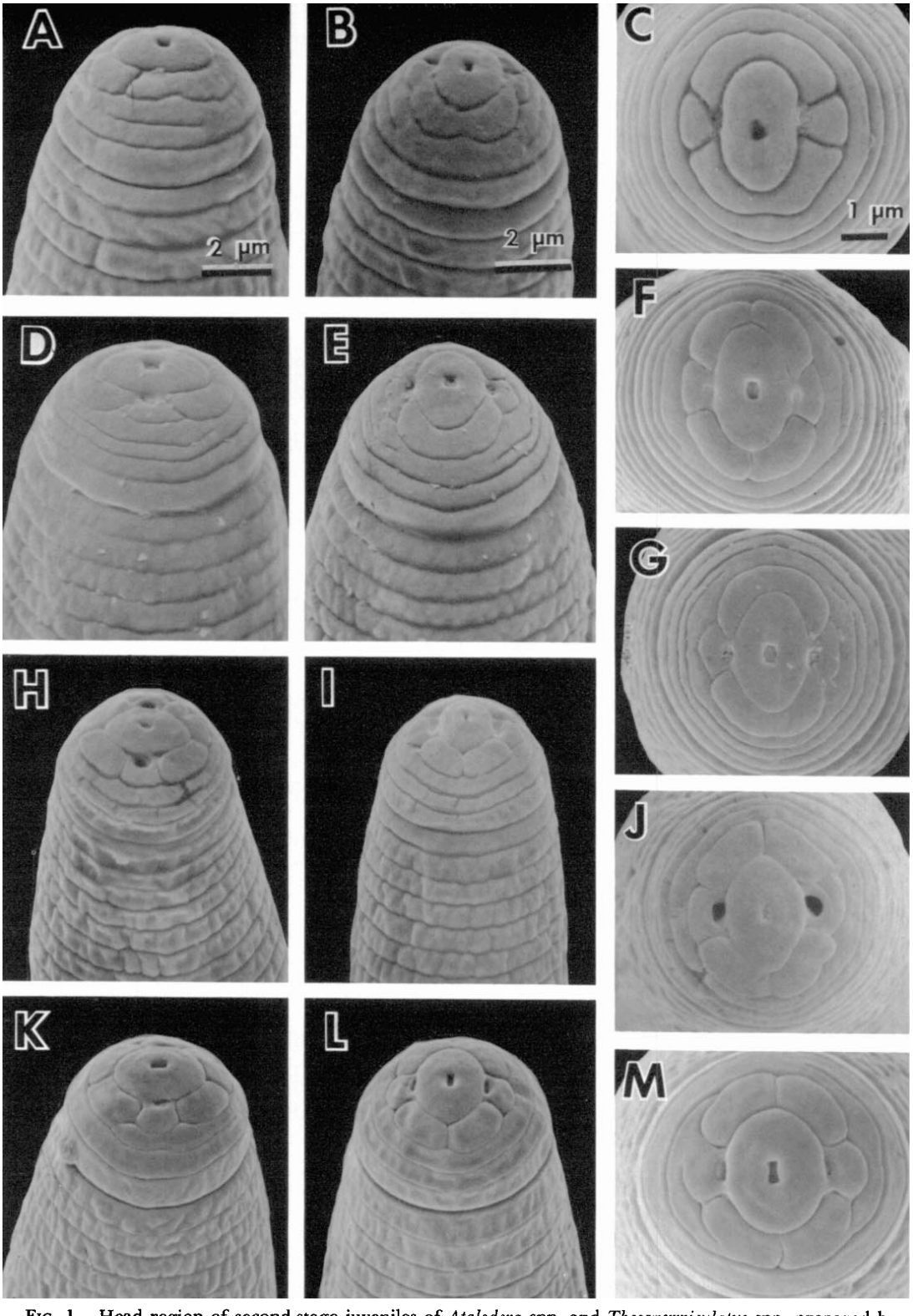

FIG. 1. Head region of second-stage juveniles of *Atalodera* spp. and *Thecavermiculatus* spp. prepared by glycerin (gly). Scales apply to each vertical column. A–C) *A. ucri.* A) Lateral. B) Medial. C) En face. D–G) *A. lonicerae.* D) Lateral. E) Medial. F) En face. G) En face. H–J) *Thecavermiculatus* sp. H) Lateral. I) Medial. J) En face. K–M) *T. andinus.* K) Lateral. L) Medial. M) En face.

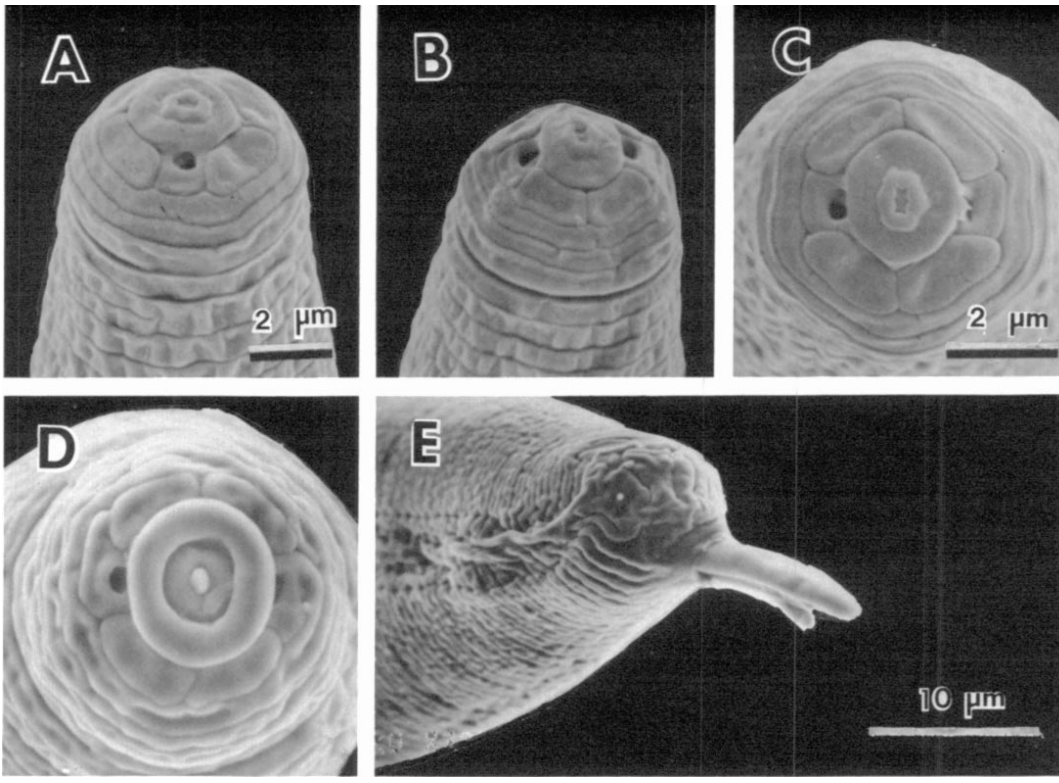

FIG. 2. Second-stage juveniles (J2) and males of *Thecavermiculatus crassicrustatus* prepared by glycerin. A–C) J2. A) Lateral. B) Medial. Scale as in A. C) En face. D, E) Male. D) En face. Scale as in C. E) Tail region.

lips are separate; the lateral lips each enclose a large amphid opening and are fused with the labial disc (Figs. 1J, M; 2C). Posteriorly the head usually has two complete annulations (Figs. 1H, I, L, K; 2A, B), although some specimens of *T. andinus* may have one incomplete and one complete annulation (Fig. 1K, M). *T. crassicrustatus* J2 are distinct within the genus by the labial disc which has a raised ring around the prestoma (Fig. 2A–C).

In *A. ucri* males the round labial disc is smooth and is surrounded by a wide annule formed by fusion of all lips (Fig. 3D). Posteriorly the head has one incomplete and two complete annulations. The incomplete annulation occurs only on the lateral sides (Fig. 3E, F), but in some individuals the head posterior to the lip annule consists of irregularly shaped large plates delimited by longitudinal and transverse incisures (Fig. 3A). The en face patterns of males of *A. lonicerae* and *Thecavermiculatus* sp. are similar. In both species the round labial disc is surrounded by six separate lips, and posteriorly the head consists of a pattern of irregularly shaped plates delimited by longitudinal and transverse incisures (Fig. 3G–L). Males of *A. lonicerae,* however, are distinguished from those of *Thecavermiculatus* sp. by the labial disc, which has a raised peripheral ring around the prestoma (Fig. 3G). In *A. lonicerae* variant males, the adjacent submedial lips are fused with each other and with the lateral lips; in addition the lateral lips may be partially fused with the labial disc (Fig. 3B). In *Thecavermiculatus* sp., however, the lateral lips are sep-

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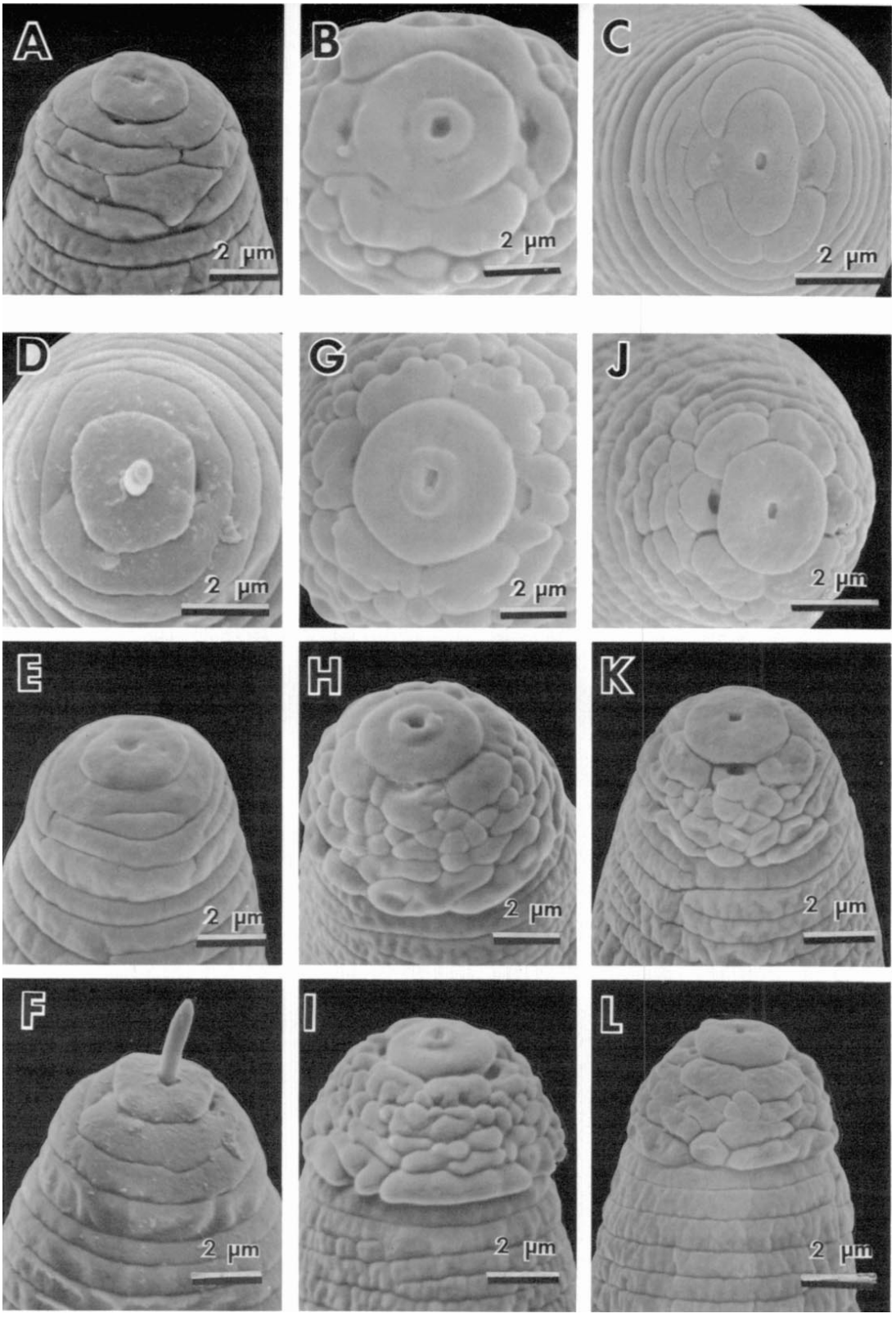
FIG. 3. Head region of variants of *Atalodera* spp. and typical males of *Atalodera* spp. and *Thecavermiculatus* sp. prepared by glycerin (gly). A–C) Variants. A) *A. ucri* male (medio-lateral). B) *A. lonicerae* male (en face). C) *A. lonicerae,* second-stage juvenile (en face). D–L) Typical males. D–F) *A. ucri.* D) En face. E) Lateral. F) Medial. G–I) *A. lonicerae.* G) En face. H) Lateral. I) Medial. J–L) *Thecavermiculatus* sp. J) En face. K) Lateral. L) Medial.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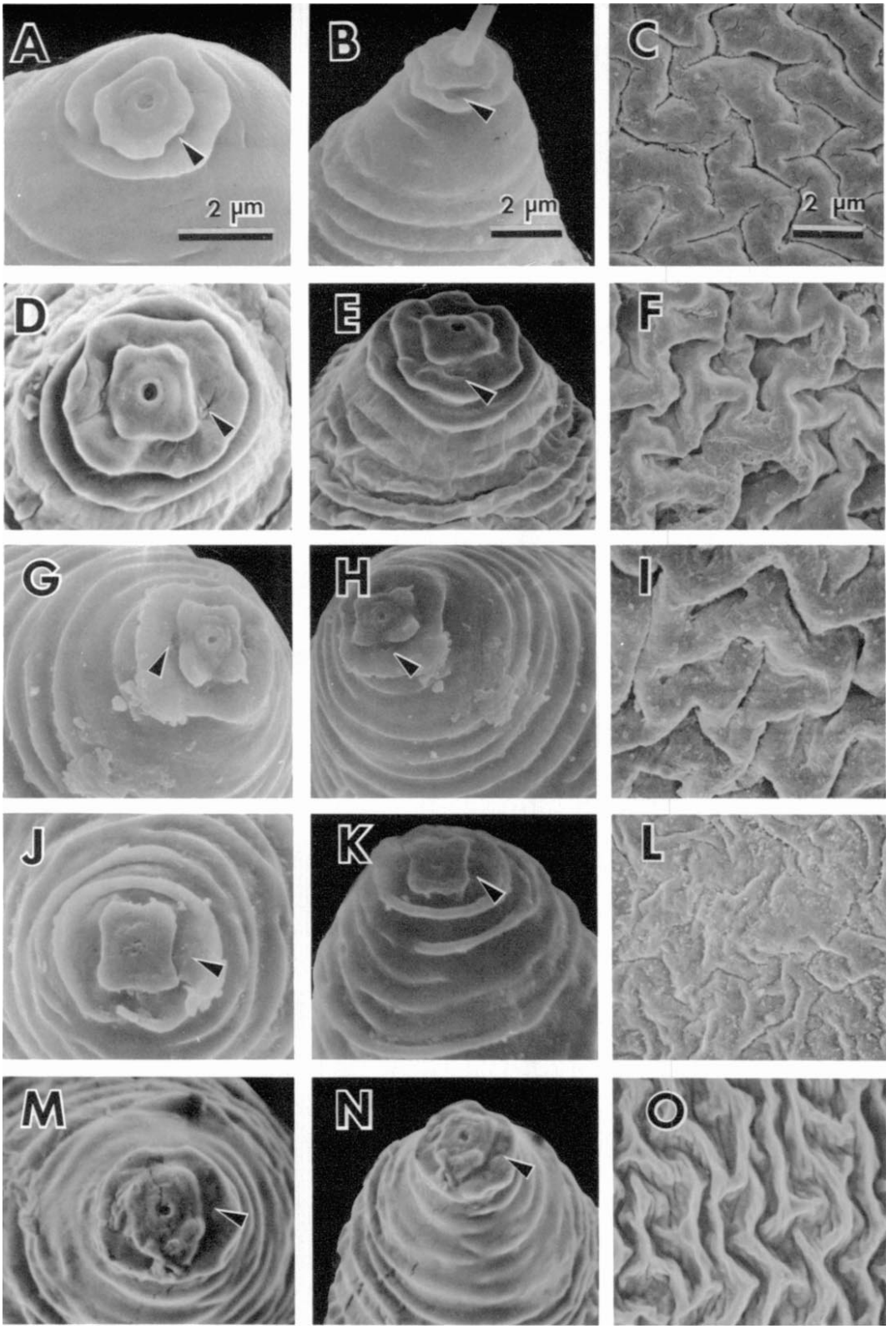
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arate from the smooth labial disc (Fig. 3J). Unlike males of *Thecavermiculatus* sp., males of *T. andinus* have at least two annulations on the head. The pattern of *T. crassicrustatus* resembles *Thecavermiculatus* sp., except the labial disc has a pronounced elevated, doughnut-like, peripheral ring and head plates are reduced (Fig. 2D).

The en face patterns of females of *Atalodera* and *Thecavermiculatus* species have a rectangular to round labial disc with a raised ring at the periphery, occupying about half its diameter. The labial disc is surrounded by a wide annule which is formed by fusion of all lips. Amphid openings are more clearly demarcated in females of *A. ucri* and *Thecavermiculatus* sp. than in females of *A. lonicerae, T. andinus,* and *T. crassicrustatus* (Fig. 4A, D, G, J, M). Posteriorly the head in these species has annules, but they differ in number and width (Fig. 4B, E, H, K, N). The annules tend to be wide in *A. ucri, Thecavermiculatus* sp., *T. andinus,* and *T. crassicrustatus* (Fig. 4B, H, K, N) and narrow in *A. lonicerae* (Fig. 4E). In *A. lonicerae* the head has four annulations of which at least one is complete (Fig. 4E). The head of *Thecavermiculatus* sp. females has about five annulations of which at least two are incomplete (Fig. 4H), whereas *T. andinus* has at least four annulations of which at least one is complete (Fig. 4K). The head of *T. crassicrustatus* females has at least six annulations of which at least three are complete (Fig. 4N).

Cuticular pattern in females: Although the cuticle patterns of females are irregular in all species, they differ by SEM details (Fig. 4C, F, I, L, O). In *A. ucri* the pattern consists of ridges separated by angular zigzag shallow crevices (Fig 4C), whereas in *A. lonicerae* the pattern is composed of a network of ridges separated by deep crevices (Fig. 4F). In *Thecavermiculatus* sp. the cuticle pattern includes broad ridges separated by deep crevices, whereas in *T. crassicrustatus* the ridges are narrow and the crevices are deeper (Fig. 4I, O). In *T. andinus* females the cuticle has a swirled pattern of superficial crevices separated by irregularly shaped ridges and mounds (Fig. 4L).

Lateral fields and phasmids: The lateral fields in J2 of *A. lonicerae* and *Thecavermiculatus* spp. include four incisures delineating three longitudinal bands; the outer bands are clearly areolated in *A. lonicerae, Thecavermiculatus* sp., and *T. andinus,* whereas in *T. crassicrustatus* all bands are areolated (Fig. 5E, H, K, N). In *A. ucri* J2 the lateral field includes only three incisures delineating two areolated bands (Fig. 5B). In all species the lateral field originates about 9–10 annules from the labial disc (Fig. 5A, D, G, J, M). In *A. ucri* J2 the lateral field begins as two incisures, with the center incisure originating about two annules posterior to the outer incisures (Fig. 5A). The lateral field in *A. lonicerae* J2 originates as two incisures; a third incisure begins about two annules posteriorly (Fig. 5D). The fourth incisure begins about 30% of the body length from the anterior end of the nematode. The lateral field in *Thecavermiculatus* sp. J2 originates as three incisures (Fig. 5G); as in *A. lonicerae* the fourth incisure begins at about 30% of the body length from the anterior end of the nematode. In *T. andinus* J2 the lateral field originates as two incisures; the remaining two incisures begin about five annules posteriorly (Fig. 5J). The lateral field of *T. crassicrustatus* originates as two incisures, and the third incisure begins six annules posteriorly (Fig. 5M). The fourth incisure begins about 30% of the body length from the anterior end of the nematode. The lateral field changes little throughout the nematode length until 5–7 annules anterior to the phasmid opening. In this region the middle band terminates in J2 of *A. lonicerae, Thecavermiculatus* sp., and *T. crassicrustatus* but not in *A. ucri* or *T. andinus* (Fig. 5C, F, I, L, O). In *A. ucri* the phasmids

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FIG. 4. Head region and cuticular pattern of females of *Atalodera* spp. and *Thecavermiculatus* spp. prepared by glycerin (gly) or critical point drying (cpd). Scales apply to each vertical column. A–C) *A. ucri.* A) En face (cpd). B) Lateral (cpd). C) Cuticular pattern (gly). D–F) *A. lonicerae* (gly). D) En face. E) Medio-lateral. F) Cuticular pattern. G–I) *Thecavermiculatus* sp. G) En face (cpd). H) Medio-lateral (cpd). I) Cuticular pattern (gly). J–L) *T. andinus.* J) En face (cpd). K) Medial (cpd). L) Cuticular pattern (gly). M–O) *T. crassicrustatus.* M) En face (gly). N) Medial (gly). O) Cuticular pattern (gly). Arrows indicate position of amphid openings.

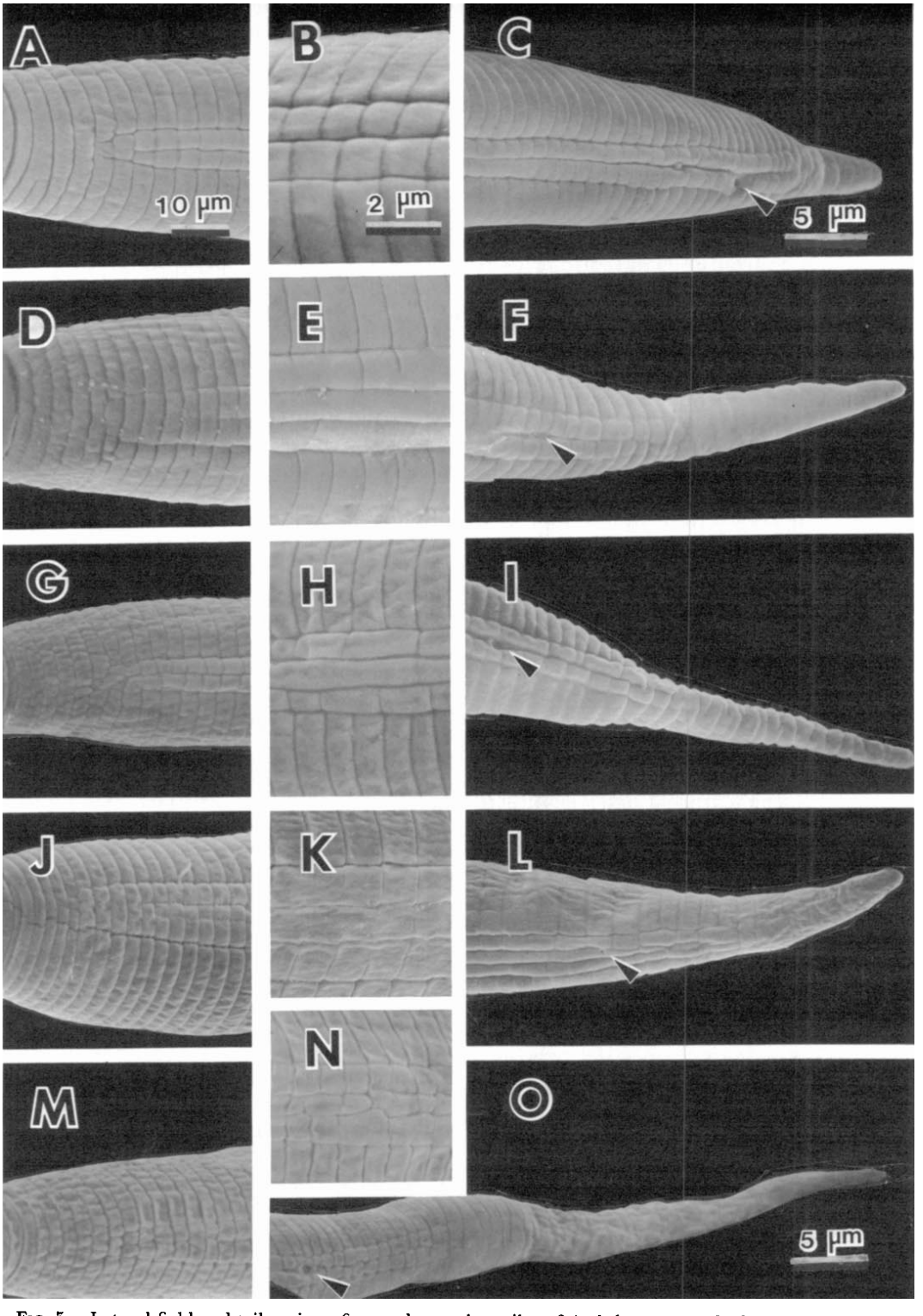

FIG. 5. Lateral field and tail region of second-stage juveniles of *Atalodera* spp. and *Thecavermiculatus* spp. prepared by glycerin (gly). Scales apply to each vertical column excluding O. A–C) *A. ucri.* A) Anterior end of lateral field. B) Lateral field at midbody. C) Tail region. D–F) *A. lonicerae.* D) Anterior end of lateral field. E) Lateral field at midbody. F) Tail region. G–I) *Thecavermiculatus* sp. G) Anterior end of lateral field. H)

open either on the dorsal band (Fig. 5C) or between the two longitudinal bands as in *A. lonicerae, Thecavermiculatus* sp., and *T. crassicrustatus* (Fig. 4F, I, O). In *T. andinus,* however, the phasmid pore occurs as a small pit in the middle longitudinal band (Fig. 5L). In *A. ucri, A. lonicerae, Thecavermiculatus* sp., *T. andinus,* and *T. crassicrustatus,* phasmids occur about 8, 8–14, 12, 7, and 18 annules before the posterior end of the lateral field, respectively (Fig. 5C, F, I, L, O).

In males of *A. ucri, A. lonicerae,* and *Thecavermiculatus* sp., the lateral field originates about 10, 6, and 7–8, annules, respectively, from the labial disc (Fig. 6A, E, I). In all species the lateral field at midbody includes three longitudinal bands; the outer bands are clearly areolated in *A. lonicerae* and *Thecavermiculatus* sp. (Fig. 6F, J), whereas they are faintly areolated in *A. ucri* males (Fig. 6B). In *A. ucri* the lateral field originates as two areolated bands (Fig. 6A), the third band beginning ca. 90 μm posterior to the labial disc. In *A. lonicerae* the lateral field originates as a single incisure and the other two incisures begin about five annules posteriorly (Fig. 6E). The fourth incisure begins about 45 μm posterior to the labial disc. In *Thecavermiculatus* sp. males the lateral field originates as two areolated bands (Fig. 6I). The third band begins ca. 22 μm posterior to the labial disc. In all species the lateral field extends as three longitudinal bands throughout the length of the nematode ending near the tail terminus (Fig. 6D, H, L). In end view, the tail in *A. ucri, A. lonicerae,* and *Thecavermiculatus* sp. is smooth and triangular in shape, the triangular shape extending to include the spicular sheath (Figs. 2E; 6C, G, K). Phasmid openings were not observed in males of any of the three species (Figs. 2E; 6C, D, G, H, K, L).

Female perineal regions: In females of *Atalodera* the perineal region of the distinct terminal prominence consists of a vulval slit surrounded by clearly marked inner vulval lips and outer vulval lips; outer vulval lips may be unequal in size and extend to cover the remainder of the prominence or cone (Fig. 7A, B). In *Thecavermiculatus* sp. females the cone is indistinct. The perineal pattern includes a vulval slit surrounded by two clearly marked, equal sized inner vulval lips. The inner vulval lips are surrounded by wide outer vulval lips which are clearly demarcated from the rest of the body (Fig. 7C). The outer dorsal vulval lip, which is wider than the outer ventral lip in *A. ucri, A. lonicerae,* and *Thecavermiculatus* sp. (Fig. 7A–C), is pitted only in *Thecavermiculatus* sp. and *A. lonicerae* (Fig. 7B, C). The narrower outer ventral vulval lip has a lace-like pattern in all the above species (Fig. 7A–C). The exact location of the anus on the outer dorsal vulval lip varies with the species. The anus is on the middle of the outer dorsal vulval lip in *A. ucri* (Fig. 7A) and on the border area between inner and outer dorsal vulval lips in *A. lonicerae* (Fig. 7B). In *Thecavermiculatus* sp. the anus is located on the one-third of the outer dorsal vulval lip nearest the inner dorsal lip (Fig. 7C). In *T. andinus* and *T. crassicrustatus* the vulval slit is surrounded by a smooth area in which vulval lips are not clearly delineated (Fig. 7D–F). In *T. andinus* the smooth area is small and surrounded by 4–5 annules, with the anus located dorsally at the margin of the annules (Fig. 7D, E). In *T. crassicrustatus* sp. the body pattern extends between the vulva and anus (Fig. 7F).

Discussion

SEM examination of J2 and adults of *Atalodera* and *Thecavermiculatus* revealed new morphological characters that can be used with additional characters in identification and in refining hypotheses of phylogenetic relationships. En face patterns of *Atalodera* and *Thecavermiculatus* sp. apparently share only primitive character states which are therefore not very useful in testing monophyly of these genera. These and other characters are nevertheless useful in understanding intrageneric relationships. For example, en face patterns of *A. ucri* J2 and of about half of the *A. lonicerae* J2 con-

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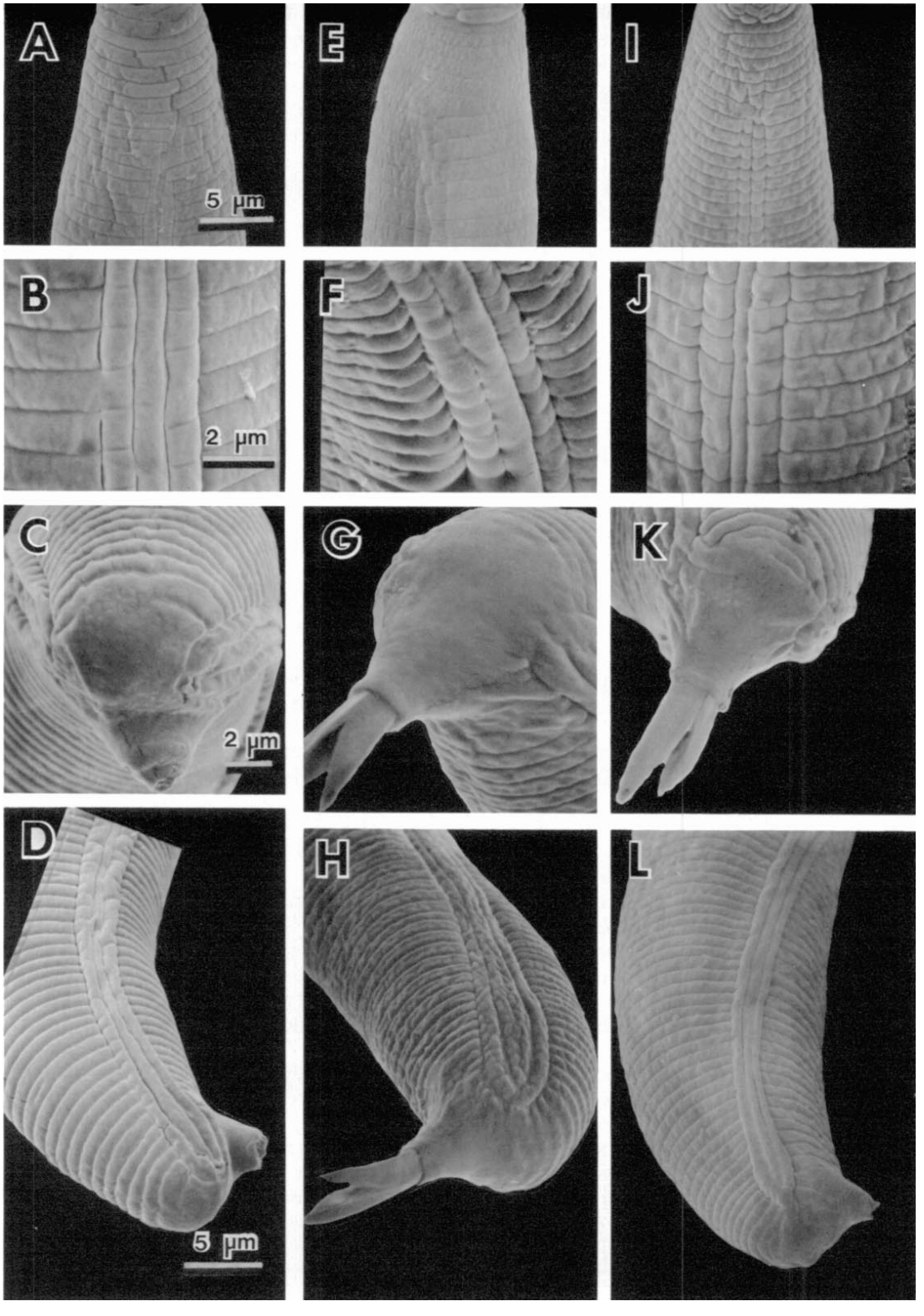
Lateral field at midbody. I) Tail region. J–L) *T. andinus.* J) Anterior end of lateral field. K) Lateral field at midbody. L) Tail region. M–O) *T. crassicrustatus.* M) Anterior end of lateral field. N) Lateral field at midbody. O) Tail region. Arrows indicate position of phasmid openings.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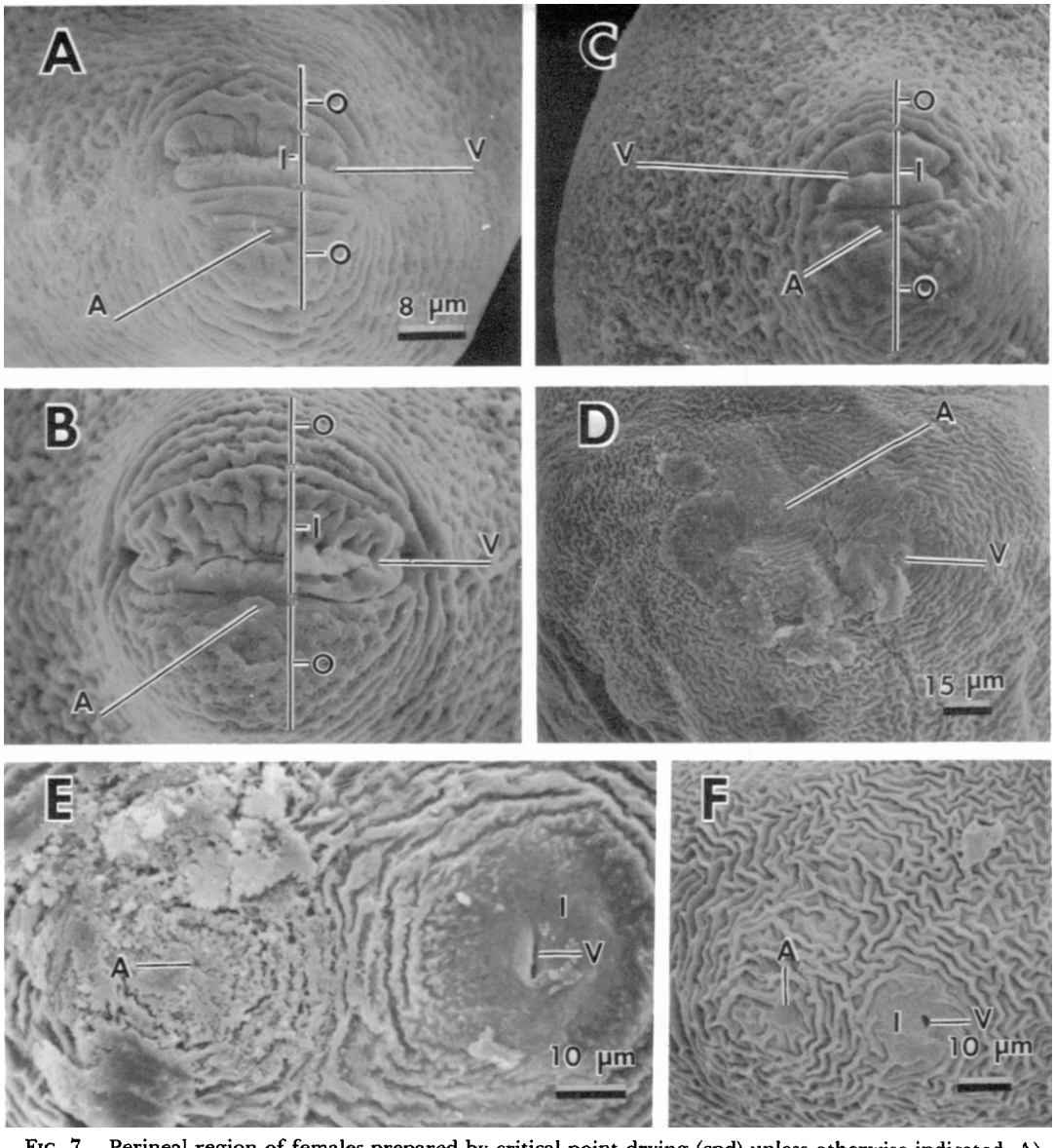

FIG. 7. Perineal region of females prepared by critical point drying (cpd) unless otherwise indicated. A) *Atalodera ucri.* B) *A. lonicerae.* Scale as in A. C) *Thecavermiculatus* sp. Scale as in A. D) Low magnification of *T. andinus.* E) High magnification of *T. andinus.* F) *T. crassicrustatus* prepared by glycerin. A = anus, I = inner-vulval lip, O = outer-vulval lip. V = vulva.

sist of a labial disc surrounded by separate lateral lips and fused adjacent submedial lips. Most of the remaining *A. lonicerae* J2 have a primitive en face pattern with six separate lips which resembles that of *Thecavermiculatus* sp. J2. Similar primitive patterns also occur in *Meloidodera* spp. (11) and *Cryphodera utahensis* (2). Furthermore, in spite of the clear difference in the en face patterns of *A. ucri* males (all lips fused) and

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FIG. 6. Lateral field and tail region of males of *Atalodera* spp. and *Thecavermiculatus* sp. prepared by glycerin (gly). Scales apply to each horizontal row. A–D) *A. ucri.* A) Anterior end of lateral field. B) Lateral field at midbody. C) End view of tail. D) Tail region. E–H) *A. lonicerae.* E) Anterior end of lateral field. F) Lateral field at midbody. G) End of view of tail. H) Tail region. I–L) *Thecavermiculatus* sp. I) Anterior end of lateral field. J) Lateral field at midbody. K) End of view of tail. L) Tail region.

A. lonicerae (all lips separate), some similarities occur. Specifically, a few variant *A. lonicerae* males have all the lips partially fused and thus are similar to *A. ucri.* In addition, irregularly shaped plates as occur on heads of *A. lonicerae* males also occur on the heads of a few variant *A. ucri* males. These findings support the decision of Luc et al. (8) to consider *Sherodera* a junior synonym of *Atalodera.* In addition, one of the diagnostic characters of *Sherodera* is the presence of striated longitudinal annules in the head region (15). Using this character to justify a separate genus, however, is further questioned since the same character occurs in *Thecavermiculatus* spp. and some individuals of *A. ucri* as well as in males of *Cryphodera utahensis* and *C. podocarpi* (2). A variation of this pattern also occurs in males of *Meloidodera charis* (11), *M. belli* (11), *C. coxi* (2), and *C. nothophagi* (2). The distribution of this trait, including its occurrence in the outgroup Hoplolaimidae, suggests it is primitive and not useful for identifying sister groups.

SEM examination of *A. ucri, A. lonicerae,* and *Thecavermiculatus* sp., as well as *T. gracilancea* (13), reveals that the female perineal region consists of a vulval slit located between clearly demarcated inner vulval lips. The inner vulval lips are surrounded by wider outer vulval lips. In these four species the anus opens on the outer dorsal vulval lip close to the vulval slit. The close position of the vulva and anus is a derived character state, relative to their wide separation (5), and thus supports the hypotheses that *Atalodera* and these species of *Thecavermiculatus* combined are monophyletic. This conclusion is further supported by additional shared derived characters, including a D layer in the body wall cuticle of females (1,4) and induction of a host response involving syncytia with pit fields but without wall ingrowths (9,10). The cuticle D layer is reported to occur in certain other Heteroderidae (9), and syncytia are also induced by cyst-forming species. Syncytia of cyst-forming heteroderids differ by the presence of wall ingrowths, however, and may have developed through convergent evolution. Questions of monophyly of *Atalodera* and *Thecavermiculatus* must also consider that *T. andinus* and *T. crassicrustatus,* which have en face patterns similar to other *Thecavermiculatus* sp., show striking differences in the posterior area of females. Females of *T. crassicrustatus* have a smooth perivulval region which lacks clearly demarcated inner vulval lips and has only traces of outer vulval lips. *T. andinus* has a similar perivulval region although it is further reduced in size, has faint inner vulval lips, and lacks outer vulval lips. Furthermore, the anus and vulva are widely separated by a mean of 59 μm in *T. andinus* (7) versus 18–19 μm in the other three *Thecavermiculatus* species (3,13). J2 of *T. andinus* are unique from other species of the two genera by the lateral field which continues to the posterior terminus as three bands with each minute phasmid opening located in the center of the middle band. In other species the middle band terminates anterior to the phasmid openings which occur between the two remaining bands. *T. andinus* is also distinct by the fine lace-like cuticular pattern in the midbody region of females, contrary to the original description which described the midbody pattern as annulated (7). In addition, the head region of males is faintly annulated in *T. andinus,* whereas it consists of irregularly shaped plates in *Thecavermiculatus* sp. and *T. crassicrustatus.* These differences may require reconsideration of the recently emended diagnosis of the genus, *Thecavermiculatus* (7).

Although species of *Atalodera* and *Thecavermiculatus* combined can generally be supported as a monophyletic group, a clearer understanding of morphology and descriptions of new species makes it increasingly difficult to diagnose *Thecavermiculatus* from *Atalodera.* Previously, these were separated on the basis of retention of J2 in females of *Thecavermiculatus* and relative prominence of the cone in *Atalodera.* However, we have frequently observed similar retention of J2 in females of non-cyst-forming heteroderids including *Meloidodera* spp., *Atalodera ucri,* and undescribed *Atalodera* sp. (unpublished observations). If intermediate species are described which indicate a clear transformation series toward reduction of the ataloderid cone, a phylogenetic classification might justify synonymy of *Thecavermiculatus* with *Atalodera.* Presently, we believe reclassification to be premature, since relationships

within this group must be considered in light of a proposed phylogenetic analysis including similar new characters for the entire family Heteroderidae.

Addendum

Subsequent to acceptance of this manuscript for publication, *Cryphodera utahensis* was placed in a new genus, *Bellodera utahensis* (Baldwin et al., 1983) Wouts, 1985, and *Thecavermiculatus andinus* was proposed as *Dolichodera andinus* (Golden et al., 1983) Wouts, 1985.

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